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ENLARGED SUCKERS AS AN INDICATOR OF MALE MATURITY IN *OCTOPUS*

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ABSTRACT

Inadequate identification of octopus age classes has severely limited field studies of their biology. Four predictions are made to differentiate males at the plateau of growth that precedes senescence, i.e., mature males, from immature males. Compared to immature males, mature males are predicted to be 1) more mobile because their reproductive fitness depends on the number of receptive females they encounter; 2) more often injured, due either to increased mobility or decreased regeneration capacity; 3) more attractive as mates due to their maturity; and 4) mature males, overall, are predicted to be larger due to their advanced age. An intertidal population of *Octopus digueti,* sampled for 1 year, provided data to test the hypothesis that males with a few conspicuously enlarged suckers represent a mature age class as characterized above. As a group, males of *O. digueti* with enlarged suckers met these expectations; therefore, the presence of enlarged suckers is concluded to accurately indicate male maturity. I suggest enlarged suckers act as chemoreceptors of chemical cues released by receptive females and thus may contribute directly to male fitness.

The typical octopus life cycle begins with a period of rapid growth, followed by a period of zero growth during which females produce their only clutch of eggs. The comparatively brief cycle ends with the onset of senescence, a terminal decline in body weight of both males and females. Despite the ease with which these stages can be characterized in laboratory studies, researchers have been unable to accurately estimate the age or relative maturity of wild-caught octopuses.

Aging octopuses by growth annuli has been not been possible (Robinson and Hartwick, 1986). Although body size is frequently used as an index of age in wild populations (Hartwick et al., 1984; Ambrose, 1988; Aronson, 1989), size may be only poorly associated with chronological age or time until senescence (Mangold, 1987). Even in carefully controlled laboratory environments, offspring from a single clutch of eggs (assumed to be half-siblings) show remarkable variation in maximum body size and life span (Forsythe, 1984; Forsythe and Van Heukelem, 1987; Forsythe and Hanlon, 1988).

Reproductive activity is also generally uncorrelated with relative maturity in octopuses. Although egg laying occupies a restricted portion of the life cycle, females are sexually receptive for an extended period before egg laying begins, as evidenced by the fact that sperm can be viably stored for at least 10 months in some species (Mangold, 1987).

The condition of the single octopus gonad provides some information about female maturity. The ovary enlarges only briefly before egg-laying, and therefore accurately indicates the onset of senescence, that is true maturation. Ovary weight, however, is not correlated with body weight across octopus populations (Mangold and Froesch, 1977; Smale and Buchan, 1981) because ovarian enlargement and egg-laying occur over a wide range of body sizes.

In contrast, testis weight is tightly correlated with male body weight throughout most of the life (Mangold and Froesch, 1977; Smale and Buchan, 1981). Actively growing males with a fully formed intromittent organ, the ligula, have an enlarged testis and are producing spermatophores which are stored in Needham's Sac (Smale and Buchan, 1981; Hanlon, 1983; Voss, 1983). Unlike the information conveyed by an enlarged female gonad, the presence of an enlarged male gonad

is virtually uninformative about the male's biological age (time until senescence) as, it appears, is the presence of spermatophores.

Several methods have been proposed to assess male maturity. These methods generally involve the use of a ratio or index, such as the number of stored spermatophores to mantle length; penis (in octopuses an internal male organ) length to mantle length; goniduct and testis weight to body weight; or goniduct weight to goniduct and testis weight (Moriyasu, 1983; Mangold, 1987). Methods based on ratios make very explicit assumptions about allometric relationships between body components but fail to either recognize (Strauss, 1985) or test the assumptions. In addition, these methods involve generalized but untested assumptions about male reproductive biology, which may be species specific. Thus, significant time expenditures and the sacrifice of many males are required to obtain results of unknown reliability.

Externally, the only overt sexual dimorphism in some species of American tropical octopuses (Voight, 1990) is enlarged suckers in males, the two to three suckers near the web margin that are conspicuously larger than adjacent suckers. Enlarged suckers occur in both males and females in some species, although their presence has drawn most attention in males. Pickford and McConnaughey (1949), based on sucker growth allometries, suggested that sucker enlargement in males of *Octopus bimaculatus* and *O. bimaculoides* coincides with the onset of maturation, or in their terminology, "puberty." Independently, Van Heukelem (1973) noted that suckers enlarged in seven captive males of *O. cyanea* immediately before the plateau in size associated with senescence. It is this criterion which defines, in the strictest sense, true maturation.

Van Heukelem (1983) also reported that suckers enlarge at about 240 days post-hatching in laboratory-reared male *O. maya*. Males have enlarged suckers for about 55 days, 19% of their 295 day mean life span. In comparison, females surviving an average of 305 days spend their last 48 days, or 16% of the life span, egg-laying, brooding or post-brooding. The similarity of the timing of sucker enlargement in males and egg-laying in females implies that these events represent comparable levels of biological maturity in males and females.

These observations and hypotheses concerning enlarged suckers, derived from species of an apparent clade of circumtropical ocellated octopuses (Voight, 1988a), must be tested on a phylogenetically distinct lineage to insure that the character is not simply a synapomorphy of one clade. If these observations are supported, that is if males with enlarged suckers are shown to be the same biological age as females with enlarged ovaries, population biology studies of many species of octopus will be greatly facilitated. As stated above, the presence of stored spermatophores does not necessarily indicate male maturity, as even comparatively young males store spermatophores. Rather it is the biological age of males, that is, whether or not they have reached the plateau of growth that precedes senescence, which defines maturity. It is in this sense that maturity is used in this paper.

To test whether enlarged suckers accurately characterize mature males, a field study was undertaken of *O. digueti* of the pygmy octopus clade (Voight, 1988a). Four predictions of features that would differentiate mature from immature males in the absence of known ages were made: (1) Mature males are predicted to be more mobile than immature males, to increase their encounters with receptive females and their fitness; (2) On average, mature males are predicted to show more injuries than immature males, due either to increased contact with predators (or cannibals) or to their reduced ability to regenerate injuries (O'Dor and Wells, 1978); (3) Mature males are predicted to be more attractive as mates to females;

because male octopuses provide only sperm to females, females might assess advanced age as a measure of genetic quality (Halliday, 1983); and (4) Mature males, on average, are predicted to have a constant body size, larger than that of immature males. If males of *O. digueti* having enlarged suckers fulfill these predictions, then enlarged suckers can be concluded to identify mature males accurately.

Materials and Methods

Octopuses were collected using the artificial-shelter technique described by Voight (1988b). Brown glass bottles were tethered in the intertidal zone of Choya Bay, Sonora, Mexico in the northern Gulf of California from May 1984 through May 1985 (Voight, 1990). During 19 spring tidal series throughout the year, octopuses resident in the bottles at collections were captured. Pooled data from the three to seven collections made at 24-h intervals during each spring tidal series constitute the individual sample periods. Because resident octopuses were removed periodically, the presence of octopuses in the bottles reflects movements of the population.

Captured octopuses were taken to the laboratory at Centro d'Estudios Desiertos y Oceanos (CEDO) and placed in seawater aquaria. Each individual was immersed in a 2–4% ethanol-seawater solution (May–Dec.) or in cold (2–10°C) seawater (Jan.–May) until sufficiently narcotized to be easily handled, and then sexed and weighed on a triple-beam balance. Males were identified by the modification of the tip of the third right arm into the ligula, females and juveniles by its absence. Octopuses without ligulae weighing over 10 g were considered to be females. Body measurements and, for males, ligula lengths were recorded with body weight and sex for each animal. To score arm injuries, any deviation from the steadily tapering arm shape, such as truncations or areas of active regeneration, was recorded for each individual. Gonad size was assessed as viewed through the translucent skin of the narcotized octopuses.

Animals were examined for the presence of enlarged suckers. Suckers with diameters as little as 0.5 mm greater than adjacent suckers were conspicuous and were considered to be enlarged.

To assess whether spermatophore production in this species was associated with sucker enlargement, 44 preserved male specimens were dissected and scored for the presence or absence of spermatophores and enlarged suckers.

To test the four predictions thought to differentiate mature from immature males, data were analyzed as follows:

(1) To assess relative movement, total captures of males with enlarged suckers were compared to those of males with normal suckers. Van Heukelem (1973; 1983) found males to have enlarged suckers only comparatively late in their lives; therefore if octopuses are equally susceptible to capture through their life cycle, males with enlarged suckers should compose only a small proportion of the sample. Increased mobility will be seen as an increased capture rate. Samples were pooled from throughout the study to reflect the entire life span. To test the distribution of body weights sampled by the trap technique, frequency distributions of the groups were compared.

(2) The total proportion of injured males with enlarged suckers and injured males with normal suckers were compared by G-test, with William's adjustment factor (Sokal and Rohlf, 1981). Preliminary analysis found no seasonal differences (Voight, 1990).

(3) Whether males with enlarged suckers are more acceptable as mates than those with normal suckers was determined by comparing ligula lengths. If females prefer older males as mates, mature males must be able to convey information about their ages to females to increase their acceptability as mates. Voight[1] describes the initial phase of courtship in *O. digueti* as consisting of a ligula display, during which females could actively reject courting males, and shows that the ligula reaches a maximum length regardless of body size. Voight (in press) hypothesized that females may assess potential mates by ligula length, a character which reaches a species-specific maximum of 5.5 mm in *O. digueti*. If females assess males by ligula length during this display, mature males should have longer ligulae than immature males. Mean ligula lengths of the two groups were compared (at $\alpha = 0.05$) by sample period.

(4) To determine whether males with enlarged suckers as a class had a constant body size larger than males with normal suckers, mean body weights of the groups were compared (at $\alpha = 0.05$) by sample period.

Results and Discussion

Incidence.—In total, 414 males were collected throughout the study. Enlarged suckers were present on males weighing as little as 5.6 g and absent on males of

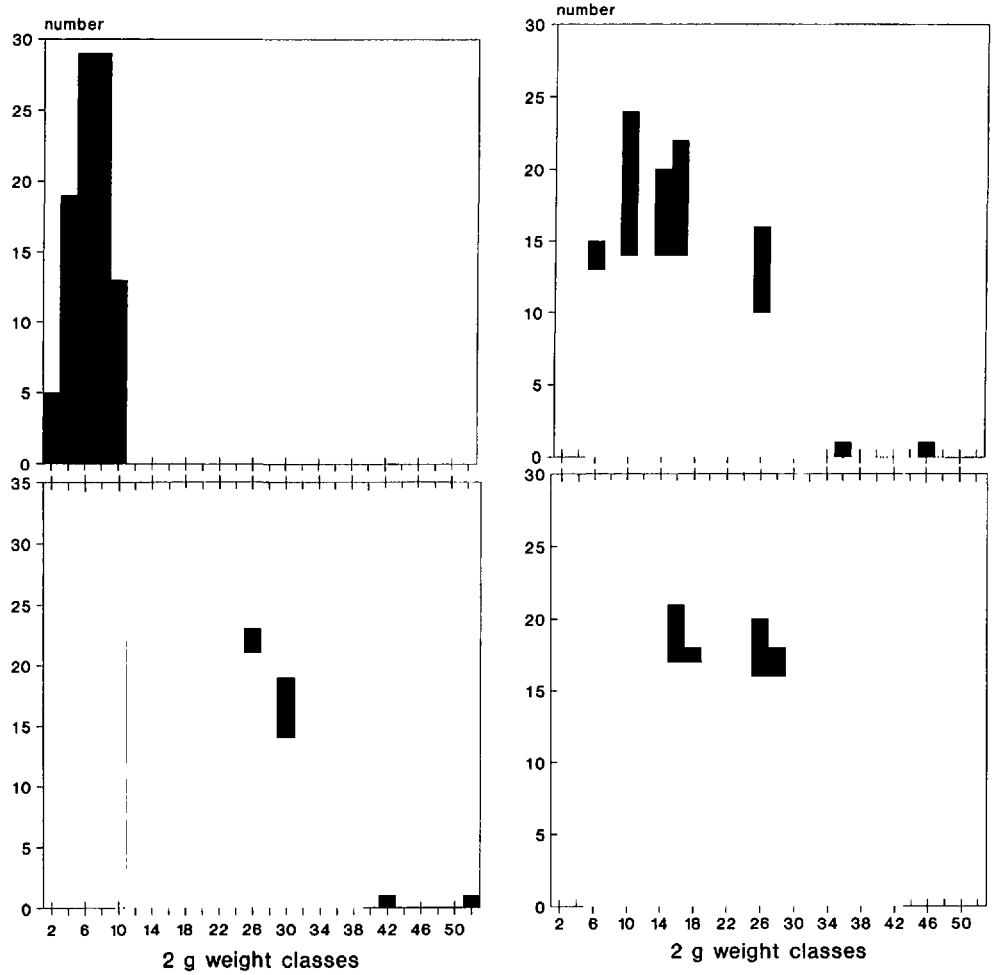

Figure 1. Frequency distribution by 2 g weight class of octopuses captured during the 1-year study. Upper left). Juveniles (weighing less than 10 g without a ligula) N = 95. Lower left). Females (weighing more than 10 g without a ligula) N = 274. Upper right). Males with normal suckers N = 211. Lower right). Males with enlarged suckers N = 203.

up to 45.6 g (Fig. 1). The diameter of enlarged suckers was as much as 250% that of the adjacent suckers.

Defining males as mature if the testis is enlarged is uninformative in this study. Over 80% of the males in 16 of 19 sample periods showed an enlarged testis; in 10 samples, 100% had an enlarged testis. Classifying males on this basis identified only males with short (<2 mm) ligulae, contributing no other information.

Spermatophores are not restricted to males with enlarged suckers in *O. digueti.* Although all males with enlarged suckers (N = 26) were storing spermatophores, most males with normal suckers were also storing spermatophores (15 of 18 individuals). In laboratory rearing studies of *O. digueti* (DeRusha et al., 1987) ligulae were first noted to have developed on day 86; 2 days later matings were observed. That spermatophores are present and that males are able to mate does not demonstrate full male maturity.

Evidence of early reproductive maturation in males (enlarged gonad, sper-

matophore presence) shows that energy allocation to reproduction differs between males and females, and may explain size dimorphism in some species (Forsythe, 1984; Forsythe and Van Heukelem, 1987). Although young males probably copulate very infrequently in nature, in cases such as very low population densities where females may face sperm limitation, males able to copulate may receive large fitness benefits and increase the likelihood of species survival.

In some species of *Octopus,* females also have enlarged suckers. Characters which enhance male fitness are also frequently present in females, due to genetic correlations (Lande, 1980 and references therein). Whether enlarged suckers indicate female maturity in these species is unknown, although the possibility merits exploration.

Mobility.—Males with enlarged suckers (N = 203) were captured as often as males with normal suckers (N = 211) (adjusted G = 0.0217; df = 1; $P > 0.05$). If enlarged suckers occur only late in the male life span of *O. digueti,* and if the trap technique provides an unbiased sample of the octopus population, the prediction that males with enlarged suckers are mature because they are more mobile is supported. All phases of the life cycle are not equally sampled by this technique; although hatching occurred in the study area, comparatively few very small octopuses were collected (Fig. 1). A strong size-bias, however, is not seen in animals over 6 g. Although males with enlarged suckers are significantly larger than males with normal suckers (see below) the groups show a similar distribution (Fig. 1), suggesting that the trap technique did not impose a significant size bias which led to this result. An independent estimate of the size distribution in the population is unavailable.

Injuries.—Males with enlarged suckers show injuries significantly more frequently (38.8%) than males with normal suckers (25.5%) (adjusted G = 27.933; df = 1; $P < 0.005$). Males with normal suckers are no more frequently injured than females or juveniles (adjusted G = 0.864; df = 1; $P > 0.05$); males with enlarged suckers show the highest injury level in the population.

O'Dor and Wells (1978) suggested that mature octopuses regenerate after injury more slowly than immature octopuses. Whether the pattern seen here is due to biochemical changes associated with impending senescence, or to increased exposure to predators, cannot be resolved with the available data.

Attractiveness.—Figure 2 shows males with enlarged suckers have longer ligulae than males with normal suckers; they therefore may be more acceptable as mates. In addition, males of *O. vulgaris* display their enlarged suckers as visual cues to females, perhaps to increase female receptivity (Packard, 1961); enlarged suckers may then also increase male mating success in this species. Although I have no evidence that enlarged suckers serve a visual function in *O. digueti,* this report reinforces the association of enlarged suckers with male maturity and increased male fitness.

Body Size.—Figure 3 shows that by sample period, males with enlarged suckers are, on average, larger than males with normal suckers and, as a group, have a relatively invariant body weight over time. One interpretation of the sequential increases in body weight of males with enlarged suckers from late June through late August is that some males in the cohort mature comparatively early (late June) at small body sizes while others grow larger, maturing as late as August or even October.

When all sample periods are pooled, the mean body weight of males with enlarged suckers (20.6 g) is significantly larger than that of males with normal suckers (16.0 g) (*t*-test; $t = 7.39$; df = 412; $P < 0.005$).

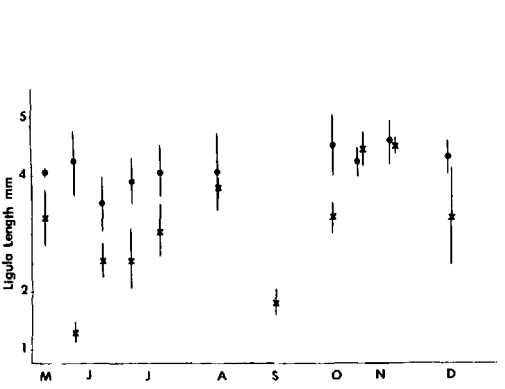

Figure 2 (left). Mean ligula lengths of males with enlarged suckers (circles) and with normal suckers (x's) which were captured from May through December. Error bars represent 95% confidence intervals.

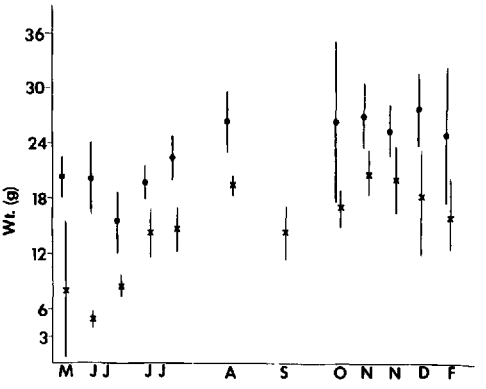

Figure 3 (right). Mean body weights of males with enlarged suckers (circles) and males with normal suckers (x's) from May through February. Error bars represent 95% confidence intervals.

In November samples, the two groups of males differ neither in body size or ligula length, as shown by the overlap of 95% confidence intervals in Figures 2 and 3. This seemingly anomalous situation is probably due to seasonal temperature changes in the northern Gulf of California (Brusca, 1980). These males matched in late summer when water temperatures reached 32°C, by the time waters cooled to 22°C in November, adult body sizes had been achieved. Body size and ligula lengthening in this cohort show acceleration due to temperature effects as have been shown in laboratory growth studies (Forsythe and Hanlon, 1988).

Generality of the Phenomenon.—Enlarged suckers, shown to be associated with male maturity in *O. digueti,* are not present in all species of *Octopus.* Species groups in which enlarged suckers are known to occur include the ocellated octopus clade, *O. bimaculatus, O. bimaculoides, O. hummelincki, O. maya, O. cyanea,* and *O. ocellatus*; the pygmy octopuses, *O. digueti, O. joubini, O. fitchi,* and *O. micropyrsus*; and about 30 other species including *O. vulgaris* (Robson, 1929; Roper et al., 1984; R. B. Toll and G. L. Voss, unpubl.).

However, the use of suckers to define maturation may not be restricted to those species currently recognized to have enlarged suckers. Sucker area may increase in at least one additional manner. Voight (1990) shows that after a minimum body size, males of *O. burryi* have suckers up to twice as large as those of females, although individual suckers are not conspicuously enlarged (Voss, 1951; Adam, 1961). In males of this species, all suckers apparently enlarge synchronously to increase the sucker surface area.

Adhesion Force.—Kier and Smith (1990) document that sucker area is a factor which determines the strength of sucker adhesion force in octopuses. If the enlarged suckers discussed here are equal in muscle density and strength to normal suckers, these suckers will exert a stronger force than do smaller, adjacent suckers. If enlarged suckers are restricted to mature animals, as is indicated, predation efficiency probably would not be significantly affected. Associated with octopus senescence is a decline in feeding which ends in death. If sucker enlargement were

associated with increased foraging efficiency, they should not be restricted to non-feeding animals.

Why Suckers?—Enlarged suckers have been suggested to play a visual role in mate recognition (Packard, 1961). When a large female *O. vulgaris* was suddenly introduced into a small male's tank, Packard reported the male's presentation of his suckers to the female as a sexual signal. However, if the visual stimulus of enlarged suckers were required to induce females to mate, octopuses not in visual contact would not copulate, as they are known to do (Wells and Wells, 1972; Forsythe and Hanlon, 1988).

Enlarged suckers probably are important in sex recognition, but rather than a visual role, I suggest they may function primarily as chemoreceptors. Sucker disks of the octopuses contain apparent chemo-receptors (Graziadei, 1964; 1965; Graziadei and Gagne, 1976). Octopuses detect water-borne chemicals (Boyle, 1983; 1986) and display chemotaxis (Chase and Wells, 1986). Suckers of severed arms distinguish acceptable from tainted food by touch (Altman, 1971).

That octopuses use chemical cues in sex recognition and mating has been repeatedly suggested, but is untested (Pickford and McConnaughey, 1949; Wells and Wells, 1972; Woodhams and Messenger, 1974; Wells, 1978; Mangold, 1983; Van Heukelem, 1983); whether the "olfactory organs" or the suckers play the more significant role in chemoreception is unknown. If receptive females release chemical cues to attract potential mates, thereby insuring fertilization of their eggs, males with a larger sucker area may be more sensitive to those cues and thus more likely to locate receptive mates. Because the number of suckers on each octopus arm appears to reach a species-specific maximum (Toll, 1988), increasing sucker size is the only available means of increasing sucker area. The apparent convergence in this character between *O. digueti* and *O. burryi* suggests a common function. Sensitivity to chemical cues may confer direct survivorship benefits to males by reducing their probability of encountering a cannibal as well as increasing their chance of mating. Future experimental testing is required to evaluate this hypothesis.

Characters which enhance fitness are likely to reliably indicate biological age. In this study, increased mobility, ligula lengthening, and increased sucker area are suggested as factors which directly increase male fitness. Because sucker enlargement is associated with these characters, enlarged suckers are useful in accurately identifying a mature male age class in *O. digueti.*

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